Report for 2003MT11B: Potamopyrgus antipodarum and baetid mayflies: temporal variation and community-level consequences

- Water Resources Research Institute Reports:
  - Cada, C. A. and B. L. Kerans. In preparation. Competitive interactions between Potamopyrgus antipodarum and baetid mayflies.
- Conference Proceedings:
  - Cada, C. A. and B. L. Kerans. 2004. Competitive interactions between the invasive gastropod Potamopyrgus antipodarum and baetid mayflies. Annual Meeting of the North American Benthological Society. Vancouver, B.C.
  - Cada, C., J. Smith, and B. L. Kerans. 2003. "What about the fish?" 3rd Annual Potamopyrgus antipodarum Conference. Montana State University - Bozeman.
- Articles in Refereed Scientific Journals:
  - Cada, C. A. and B. L. Kerans. Submitted. Community response to Potamopyrgus antipodarum invasion. Biological Invasions.
  - Cada, C. A., B.L. Kerans, and J. Smith. In preparation. Trophic effects of the New Zealand mud snail, Potamopyrgus antipodarum, on trout and a sculpin.

Report Follows

Abstract

We investigated the consequences of the introduction of *Potamopyrgus antipodarum* to Darlinton Spring Creek (Gallatin County, Montana), a popular trout spring-creek fishery where *Potamopyrgus* was recently introduced and their range has expanded. Our overall goal was to examine if and how *Potamopyrgus* changes macroinvertebrate and periphyton assemblages and whether growth of *Salmo trutta*, *Cottus bairdi,* and *Oncorrhynchus mykiss* differs between stream reaches with varying *Potamopyrgus* abundances. We examined *P. antipodarum* and baetid mayfly densities and biomasses, as well as periphyton biomass and fish diet and growth in reaches containing high and low densities of *P. antipodarum.* We also determined the strength of competitive interactions between *P. antipodarum* and baetid mayflies using two *in situ* competition experiments. Densities of baetid mayflies did not respond as strongly to high-densities of *Potamopyrgus* as we expected, and we observed no statistically significant differences in baetid density between high and low snail density reaches. *Potamopyrgus* exerted a negative effect on periphyton biomass, the hypothesized resource for which competition between *Potamopyrgus* and baetids occurs, but we did not observe a clear difference between *Potamopyrgus* and *Diphetor* or *Baetis* in their abilities to depress periphyton biomass. In competition experiments, baetid mayflies negatively affected *Potamopyrgus* survivorship but not growth. Similarly, *Potamopyrgus* negatively affected the survivorship but not the growth of the mayflies *Diphetor hageni* and *Baetis tricaudatis*. In the fish growth experiments, *C. bairdi* lost less weight in low densities of *P. antipodarum* compared to high densities of *P. antipodarum.* On the other hand, there was no difference in mean growth for *S. trutta* or *O. mykiss* between low and high densities of *P. antipodarum.* We found only 1 *Potamopyrgus antipodarum* in 1 stomach of *S. trutta in 2003* and 2 out of out of 15 contained *P. antipodarum* in 2004. However, *P. antipodarum* was eaten frequently by *O. mykiss* and sometimes in large quantities (up to 27 *P. antipodarum* per individual).

Statement of water problem:

Nonindigenous species pose one of the largest threats to biodiversity and are a major cause of endangerment or extinction of native species (Coblentz 1990, Jenkins 1996). Invasive species seriously threaten the integrity of ecosystems by altering interactions among species (Crooks 2002). For example, invasive predators can change the dynamics among resident predators and their prey, and invasive competitors can displace resident species. Such changes in interactions among species may propagate to other levels of biological scale altering population, community and ecosystem dynamics (e.g., the zebra mussel; Rappaport and Whitford 1999).

The New Zealand Mud Snail, *Potamopyrgus antipodarum*, has recently invaded freshwater ecosystems in the United States including southwestern Montana (Zaranko et al. 1997; Hall et al. 2003; Kerans et al. 2005). The high densities, feeding ecology, and reproductive biology of *Potamopyrgus* suggest that it will compete with other grazing macroinvertebrates potentially causing detrimental effects to other trophic levels including fish populations (e.g., Haynes and Taylor 1984, Dorgelo 1987, Fox et al. 1996). In addition, invasive species cost the American economy about $137 billion per year (Pimentel et al. 2000). *Potamopyrgus antipodarum* might be detrimental to local economies such as the fly-fishing industry in the Bozeman area which generates about $3.5 million annually (The River's Edge, Bozeman).

We investigated the consequences of the introduction of *Potamopyrgus* to Darlinton Spring Creek (Gallatin County, Montana), a popular trout spring-creek fishery. *Potamopyrgus* was recently introduced into the creek where their population has increased and their range has expanded. Darlinton is an ideal location to study the effects

of this invader because it supports a simple aquatic community amenable to experimental manipulation and because reaches with similar habitat properties contain varying abundances of *Potamopyrgus*. Thus, we were able to compare aquatic assemblages under varying stages of invasion but where the habitat was similar. Furthermore, our earlier, less extensive studies showed that macroinvertebrates and grazer food resources declined as *Potamopyrgus* abundances increased (Cada and Kerans, submitted).

Research Objectives:

Our overall goal was to examine if and how *Potamopyrgus* changes macroinvertebrate and periphyton assemblages and whether fish growth differs among areas with varying *Potamopyrgus* abundances. Our specific objectives were: 1) quantify the differences in the abundances of grazing mayflies as abundances of *Potamopyrgus* varies, 2) quantify the magnitude of inter- and intraspecific competition between grazing mayflies and *Potamopyrgus* varies, 3) determine how periphyton biomass changes as abundance of *Potamopyrgus* varies, and 4) explore whether insectivorous fishes fed on *Potamopyrgus* and whether growth of those fishes was lower in areas where the abundances of *Potamopyrgus* was high.

Methods:

We conducted this study in Darlinton Spring Creek at the Montana Fish, Wildlife and Parks Cobblestone fishing access site in south-central Montana, USA (45.8638°N, 111.4947°W). We have conducted research in the past in this area (Cada and Kerans submitted) and found that baetid mayflies, which were dominant members of the

scraper/collector-gather functional feeding group of the macroinvertebrate community, declined in abundance in the presence of *Potamopyrgus* (Cada and Kerans submitted). Thus, in this more extensive study, we examined how *Potamopyrgus* influenced mayflies in the family Baetidae.

 Objective 1: Macroinvertebrate field sampling—We examined *P. antipodarum* and baetid densities and biomasses in reaches with high and low densities of *P. antipodarum.* We expected baetid density and biomass and periphyton biomass to be greater in low-snail than in high-snail reaches. Both macroinvertebrate and periphyton samples were collected monthly (April 2002 to May 2003, plus July, August and October 2003) from two downstream high-snail reaches and two upstream low-snail reaches. We sampled macroinvertebrates using cobble samples to target the collecting/grazing community (Kerans et al. 1995), which we expected to be most influenced by *P. antipodarum*. Thirty-two cobbles, 8 per reach with 2 reaches per snail density, were taken each sampling date. To reduce loss of organisms due to drift when disturbed, we placed a Surber sampler (132-μm-mesh) downstream of the rock and then gently lifted both in unison from the water (Kerans et al. 1995). Cobbles were brushed and rinsed to remove organisms, which were then preserved in Kahle's solution (Pennak 1978). Dimensions of cobbles were measured according to Graham et al. (1988) for subsequent calculation of surface area and macroinvertebrate density.

We identified and enumerated invertebrates to species using a dissecting scope at 6.3X to 40X magnifications (Merritt and Cummins 1996). We calculated densities for each sample by dividing the taxa abundance by surface area of the corresponding cobble.

For baetids, we measured head capsule width to 0.01mm using an ocular micrometer at 40X magnification of randomly chosen individuals (n=20 per species per reach and sampling date), categorized individuals into developmental stages based on wing-pad size (I, II, III, or IV) as defined by Deluchi and Peckarsky (1989), and recorded sex of stage III-IV individuals based on the presence of the enlarged second pair of compound eyes of males (Peckarsky et al. 1993). We measured shell length similarly to baetid head widths and determined both reproductive status and fecundity by dissecting randomly chosen *P. antipodarum* (n=40 per reach and sampling date). Reproductive status was defined as the presence or absence of embryos in a brood pouch, whereas fecundity defined as a count of embryos present in the brood pouch.

To satisfy assumptions of normality and equality of variance, density data for all species were transformed using the natural log of x + 1, where x represents any datum point. All statistical analyses were performed using SAS 9.0 for Windows (SAS Institute Inc., Cary, North Carolina, USA). To evaluate densities and biomasses of *P. antipodarum* and baetid species and the biomass of periphyton, we used repeated measures, nested 2-way MANOVA (Von Ende 2001) with the response variable repeated over time. The 2 main factors (levels listed in parentheses) included snail-density (low or high) and reach (A or B) nested within snail-density. We were particularly interested in the time*snail interaction to determine whether the snail effect differed across time for any of the response variables.

Objective 2: Periphyton food resources —We compared periphyton biomass between high and low-snail reaches using chlorophyll *a* from small cobbles. We collected 8 additional cobbles per reach per sampling date, which were frozen and stored in the dark

until chlorophyll extraction. We extracted chlorophyll *a* in 90% ethanol by submerging each cobble and using spectrophotometric analysis to measure concentration (Cada and Kerans, submitted). Direct extraction of chlorophyll *a* was chosen over other periphyton sampling methods such as scraping or brushing of the cobbles primarily because these methods can underestimate biomass through loss of tightly adhered diatoms (Aloi 1990, Cattaneo and Roberge 1991). Biomass was calculated as the product of the extract's concentration and volume divided by the estimated surface area. We estimated surface area of the cobbles as noted for macroinvertebrates. Chlorophyll *a* and pheophytin biomasses were analyzed in the same manner as macroinvertebrate densities using repeated measures nested 2-way ANOVA.

Objective 3: Competition experiments— To determine the strength of competitive interactions between *P. antipodarum* and baetid mayflies, we conducted two *in situ* experiments in artificial chambers stocked with various density combinations of baetid mayflies and *P. antipodarum* in late summer (28 July – 13 August 2003, Experiment 1) and early winter (23 October – 11 November 2003, Experiment 2) to compare the magnitude of competition between seasons. Experiments occurred in different seasons (summer and winter) to compare the magnitude of competition between seasons. Experiment 1 was 4 days shorter than Experiment 2 because invertebrate growth is temperature dependent and body growth of individuals should have accumulated more quickly in Experiment 1. Additionally, because emergence increased over time in Experiment 1, we wanted to limit the loss of mayflies before sample size became too small.

The circular chambers were 11 cm in diameter x 14 cm in depth with two 4 x 7 cm holes covered by 500-µm nytex mesh on opposing sides of the chamber to allow water exchange. Chambers were mounted in polystyrene floats (1.2 m x 0.6 m x 0.05 m, 4 chambers per float) that were secured in the stream channel with rebar and protected from debris by 0.64 cm wire-mesh attached to the rebar upstream of the floats. Each chamber received 3 similarly sized pebbles (total surface area of about 125 cm^2) prior to invertebrate stocking. We collected the pebbles from the stream channel and carefully removed visible invertebrates to minimize disturbance of periphyton. Extra pebbles were collected and frozen for analysis to determine periphyton biomass at the beginning of the experiment (n=4 for Experiment 1 and n=18 for Experiment 2). We measured water velocity at the upstream and downstream edges of each float and at two depths (0.6X channel depth and 5 cm below the water's surface, which corresponded with the depth of the water-exchange holes) with a Swoffer 3000 flow meter. Onset® temperature probes, secured at the upstream-most and downstream-most floats, recorded water temperature at 1-hr intervals throughout the experiments.

Stocking abundances reflected the range of densities observed at Darlinton Spring Creek (10,000-20,000 m^{-2}). In Experiment 1, we compared *Diphetor* and *Potamopyrgus*, whereas in Experiment 2, we compared *Baetis* and *Potamopyrgus*. We used *Diphetor* rather than *Baetis* in Experiment 1 because most *Baetis* I collected were too small and might have escaped the chambers, but *Diphetor* was within the appropriate size range. Experiment 1 examined competitive interactions where intra- and interspecific competition cannot be separated (Goldberg and Scheiner 2001) and consisted of 3 treatments in an substitutive design where the total number of individuals in a replicate

was constant at 250: *Diphetor* alone (D), *Potamopyrgus* alone (P), and *Diphetor* plus *Potamopyrgus* together (D+P). In contrast, Experiment 2 estimated both intraspecific and interspecific interactions and was comprised of 7 treatments in a response-surface design (Table 1). Assignment of treatments to chambers was completely randomized across floats.

Invertebrate stocking of the experimental chambers occurred over 2 d. We collected invertebrates using kick nets and pipetted a known number of individuals into temporary containers. We chose *P. antipodarum* ~2 mm length and young baetid nymphs (wing-pads present but not darkened or thickened) for stocking. These sizes precluded prior embryo development by *P. antipodarum* (Richards et al. 2001) in addition to allowing growth by both species and field identification.

Maintenance of chambers and floats occurred every ~3 days. We cleaned the nytex and wire meshes of debris to aid water exchange and removed dead invertebrates by pipetting to prevent deterioration of water quality. For Experiment 2, maintenance included removal of snow and ice from the surfaces of chambers and floats. At the end of each experiment, we enumerated and preserved live individuals in Kahle's solution. Additionally, pebbles from the experimental chambers (n=3 per chamber) were frozen for chlorophyll and pheophytin analysis and calculation of periphyton biomass (see methods in field surveys).

We quantified the effect of competition using two characters related to fitness—daily survivorship and daily per capita body growth. Because *Potamopyrgus* reproduced in some replicates in Experiment 1, the response variable in that case is per capita

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population growth rather than survivorship. We calculated survivorship or per capita population growth according to equation 1.

Daily survivorship or per capita population growth =

$$\text{Eq.1}$$

ln[(final number of species y alive at experiment end)/(initial number of species y added at the beginning of the experiment)] / (number of days in experiment)

In Experiment 1, survivorship of *Diphetor* was corrected for loss of individuals due to emergence (i.e., mean daily emergence was added to each final abundance).

We calculated the second fitness characteristic, daily per capita growth, for both species according to equation 2.

Daily per capita body growth =

$$\text{Eq. 2}$$

ln[(biomass of species y alive at experiment end)/(biomass of species y added at the beginning of the experiment)] / (number of days in experiment)

To estimate initial and final biomasses, we measured shell length or head-capsule width and converted these measurements to dry-mass according to equations 3 from Cada and Kerans (submitted) and 4 from Benke et. al (1999).

Potamopyrgus dry weight [mg] = length [mm]$^{2.3697}$ * 0.117   Eq. 3

Diphetor or *Baetis* dry weight [mg] = width [mm]$^{3.326}$ * 1.2688   Eq. 4

For initial biomass, we measured 40 individuals per species, which we subsampled from the individuals available for stocking. For final biomass, we measured up to 40 individuals per species per replicate, depending on survivorship of the invertebrates.

In Experiment 1, we used 1-way ANOVA to test for a treatment effect for each response variable (survivorship and growth) for each competitor. Factor levels were *Diphetor* alone (D) or *Potamopyrgus* alone (P) and *Diphetor* plus *Potamopyrgus* (D+P). Because the response variables were not independent of each other, we used Bonferroni corrections. Additionally, we compared overall survivorship and growth between competitors using two-sample t-tests. To determine whether treatment-levels affected chlorophyll *a* or pheophytin biomass through differential grazing pressure, we used 1-way ANOVA with 5 factor levels. This analysis included an "initial" factor level that represented periphyton from the stream channel at the start of the experiment and a "control" factor level that represented periphyton biomass from experimental chambers with no invertebrates, in addition to the invertebrate treatments D, P or D+P. Chlorophyll *a* and pheophytin data were ln transformed

In Experiment 2, we used 2-way ANOVA for each competitor for each response variable with treatment ("solitary" or "B+P") and density ("low" or "high") as the factors. Because the response variables were not independent of each other, we used Bonferroni corrections. We compared overall survivorship and growth between competitors using two-sample t-tests.

Objective 4: Fish feeding and growth— We examined whether fish fed on *Potamopyrgus* and estimated the effects *P. antipodarum* density (referred to as "low snail" or "high snail") on the growth rates and body condition of *Salmo trutta, Cottus bairdi,* and *Oncorhynchus mykiss* using *in situ* enclosure experiments in 2003 and 2004. Enclosures were constructed from 2.5 x 2.5 cm pine frames to dimensions of 61 x 61 x 30.5 cm for *C. bairdi* and 61 x 91.5 x 91.5 cm for *S. trutta* and *O. mykiss.* They were wrapped with

0.85 cm nylon-netting or 0.64 cm hard-wire cloth, respectively. Bottoms and tops of

enclosures were covered with nylon window-screening, except the enclosures in 2004

were covered with hard-wire cloth. All mesh was secured with staples. In 2003, a total

of 6 brown trout enclosures and 6 sculpin enclosures were placed in high-snail and low-

snail reaches. In 2004, we placed 6 brown trout and 6 rainbow trout enclosures in high-

snail and low-snail reaches. We placed trout enclosures so that water would flow through

the chambers, but we also added several large cobbles to provide a flow-refuge

(Wilzbach et al. 1986). In 2004, we added pebbles and cobbles to cover the bottoms of

the enclosures, and we secured bundles of live willow (*Salix* sp.) branches in the front of

the enclosures to add additional refugia for fishes. Sculpin enclosures were placed in

riffles and the bottom was covered with pebbles to simulate their habitat preference.

Both enclosure types were secured to rebar posts driven into the streambed. The rebar

posts, about 30 cm upstream of each enclosure, also supported chicken-wire that served

to reduce clogging of the enclosures' mesh and improve water flow within enclosures.

All mesh, including that on the enclosures, was cleaned of debris every 2-3 days

throughout the duration of the experiment. We measured water flow at the front and rear

of each enclosure using a Swoffer 3000 and measured physicochemical water conditions

at each enclosure using a Yellow Springs Instrument (YSI).

     We collected one-year old *S. trutta* (~7 cm length) and *C. bairdi* (7-12 cm length)

by electrofishing 1 July 2003. We electrofished for *S. trutta* on 29 June 2004. We

obtained four month old *O. mykiss* (Eagle Lake strain) from the National Fish Hatchery

in Ennis, MT on 22 June 2004. Fishes were anesthetized using MS-222 for handling.

For each individual, we measured fork length (nearest mm) and wet mass (nearest 0.1g)

at the beginning and the end of the experiment (Wilzbach et al. 1986). Three sculpin per enclosure were stocked 1 July 2003, and 5 *S. trutta* per enclosure were stocked on 2 July 2003, after being held overnight within Darlinton Spring Creek. We stocked 5 *S. trutta* and 5 *O. mykiss* per enclosure in 2004. Because high flow events between 9 July and 14 July 2003 washed-out two trout enclosures (one high-snail and one low-snail), individuals were redistributed within their snail-treatment and enclosures thereafter contained only 3 trout. We terminated the sculpin experiment on 31 July 2003 and the first trout experiment on 6 August 2003. The experiments in 2004 were terminated 9 August (*O. mykiss*) and 17 August (*S. trutta*).

To determine how diet of *C. bairdi*, *S. trutta*, and *O. mykiss* differed between high-density and low-density snail reaches and to determine the extent to which *P. antipodarum* was fed on, we used gastric lavage to remove the stomach contents of all individuals (Bowen 1983) after collection or when the experiment was terminated. Invertebrates with at least a head capsule present were identified to family. Diet composition was calculated as both the relative abundance of invertebrates in the diet and the frequency of fish containing each invertebrate family.

We estimated daily growth of *S. trutta, O. mykiss* and *C. bairdi* as the difference in weight from the start and end of the experiment divided by the number of days in the experiment. Growth was transformed by ln (x + 1). We used 2-way ANOVA to compare the difference in growth between species (levels: sculpin and brown or rainbow and brown) and between snail-treatments (low and high density).

To determine the density of *Potamopyrgus* during the experiments, we sampled macroinvertebrates from low-snail and high-snail reaches on 9 July and 6 August 2003 as

well as 30 June and 19 August 2004. Additionally, macroinvertebrate densities within sculpin enclosures were sampled using cobble samples (n=3 per enclosure) as noted earlier.

Principal Findings:

Objective 1: Macroinvertebrate field sampling —*Potamopyrgus* densities peaked during summer months of 2002 (24,750 m^{-2}) but reached their lowest levels in spring 2002 and 2003 (< 1000 m^{-2}) (Figure 1, Table 2). In general, densities were lower in 2003 than in 2002, perhaps because of the biology and life history of *Potamopyrgus* or as a consequence of invasion dynamics. *Potamopyrgus* may be sensitive to cold temperatures (Hylleberg and Siegismund 1987) and an early, particularly low-temperature event may have decreased survival of individuals in late winter and early spring 2003. In support of this hypothesis, minimum and maximum temperatures in October were nearly three degrees cooler in 2002 than in 2003 (2.76-14.11 ºC and 5.42-17.59 ºC, respectively). Alternatively, many invasive species exhibit dynamic population behavior with large cycles or experience a "boom and bust" where populations decline markedly after initial high abundances (Williamson and Fitter 1996). However, large intra-annual changes in densities have been observed for this species (Dorgelo 1987, Schreiber et al. 1998), suggesting population density variation may have been within the normal range for *P. antipodarum*. For example, density in Darlinton Spring Creek dropped from nearly 28,000 m^{-2} in November 2000 to almost 9,000 m^{-2} in June 2001 (Cada and Kerans, submitted). *Potamopyrgus* reproduced year-round and did not exhibit clear cohorts, which is consistent with other findings on *P. antipodarum* reproduction

(Winterbourn 1970). Thus, it seems more likely that this population fluctuates temporally as some function of the winter environment (e.g., low temperature, low productivity).

All three mayfly species exhibited patterns of abundance and size-class distributions consistent with univoltine life cycles (Figure 2, Table 3). Young *Baetis* individuals (stage I) formed a large proportion of the population as early as July and were the dominant life stage in fall and early winter. *Baetis* individuals close to emergence and maturity (stage IV) were present over a wide range of months from late-winter through mid-summer suggesting that emergence occurred throughout these months and was not tightly synchronized. In contrast with *Baetis*, young *Diphetor* and *Acerpenna* individuals did not comprise a large proportion of the population until September and consisted of more than 90% of the population through February. This indicates eggs began hatching in late summer and may have continued throughout winter. In addition, little if any individual growth occurred during winter months as mean head width did not change during that time period. Stage IV individuals of *Diphetor* and *Acerpenna* occurred from late spring throughout the summer, indicating emergence occurred primarily in summer months and *Diphetor* may have emerged slightly before *Acerpenna*. Differential timing of emergence between *Diphetor* and *Acerpenna* may be caused by different developmental requirements such as degree days or could be a result of past competitive interactions and temporal habitat partitioning (Connell 1980).

Densities of baetid mayflies did not respond as strongly to high-densities of *Potamopyrgus* as we expected (Figures 1 and 2, Tables 2 and 3); i.e., we expected mayfly densities to be higher in low-snail reaches than in high-snail reaches at least during fall

months as we observed in November 2000 for a similar magnitude of snail densities (Cada and Kerans, submitted). High variability undoubtedly decreased our ability to detect statistical differences between mean mayfly densities in high-snail and low-snail reaches.

While there were no statistical differences in mayfly densities between high and low snail reaches, we think it worthwhile to explore the trends observed because they may be biologically significant. *Baetis* densities appeared greater in low-snail reaches than in high-snail reaches during late winter and relatively late within larval development (Figure 3). *Diphetor* densities tended to be greater in low-snail reaches than in high-snail reaches in late fall and early winter, before larvae began to develop wing pads. In contrast to *Baetis* and *Diphetor*, *Acerpenna* seemed to be positively affected (densities greater in high-snail reaches than in low-snail reaches) beginning in late fall and continuing through early spring. These trends suggest that the interaction between *Potamopyrgus* and baetids may be biologically significant at certain time periods. Additionally, these trends agree with previous field research that showed a strong effect of *Potamopyrgus* on the density and biomass of baetid mayflies in November 2000 (Cada and Kerans, submitted).

It is important to point out that "high" *Potamopyrgus* densities within our field study do not represent the range of densities that *Potamopyrgus* reaches in other locations (Kerans et al. 2005, Hall et al. 2003). In a broader perspective, the densities observed in Darlinton Spring Creek would more correctly be considered "moderate". As a result, the effect of *Potamopyrgus* on baetid mayflies in locations of "high" (i.e., > 50,000) and

extremely high (i.e., > 150,000) densities could be much stronger and more apparent than we observed in this study.

Objective 2: Periphyton food resources —In the field survey, both chlorophyll a and pheophytin a biomasses varied over time and seemed to reach the greatest biomass in fall months (Figure 3; Table 4). Chlorophyll a was marginally higher in low snail density reaches than in high-snail density reaches (Figure 3; Table 4, snail effect, $P < 0.06$). Since we did not observe a clear effect of *Potamopyrgus* on baetid mayflies in the field study, it seems likely that *Potamopyrgus* did not depress resources sufficiently to limit resources and strongly influence baetid densities. Periphyton is probably not the only resource for which *Potamopyrgus* may compete with baetid mayflies. Space is likely to be an important factor because high densities of *Potamopyrgus* should limit habitat availability.

In Experiment 1, Chlorophyll a and pheophytin biomasses were greater in the initial and control treatments than in D, P or D+P treatments (chlorophyll a: $F_{5,19} = 8.58$, $P = 0.0004$; pheophytin: $F_{4,19} = 11.58$, P <0.0001; Tukey's HSD P < 0.05) (Figure 4). *Potamopyrgus* and *Diphetor* did not differ in their effect on periphyton biomass (Figure 4).

In Experiment 2, mean chlorophyll a biomass was somewhat lower in *Baetis*-only treatments (Figure 5) (species: $F_{2,92} = 2.73$, P = 0.0703) in comparison to the initial and control levels as well as to *Potamopyrgus*-only and B+P treatments, indicating that chlorophyll a biomass was depressed in the experiment only when *Baetis* grazed by itself. Density did not affect chlorophyll a biomass (density: $F_{1,92} = 0.01$, $P = 0.9396$; species*density: $F = 1.98$, $P = 0.1432$). Similarly, mean pheophytin a biomass was lower

in *Baetis*-only treatments (species: $F_{2,92}$ = 4.25, P = 0.0172) in comparison to all other

treatment levels, indicating that only grazing by *Baetis* was able to depress pheophytin

biomass lower than the initial and control levels of biomass. An interaction effect

indicates that pheophytin *a* biomass was lower in the high B+P treatment in comparison

with the low B+P treatment (density: $F_{1,92}$ = 0.10, P = 0.752; treatment*density: $F_{2,92}$ =

4.43, P = 0.0145). Additionally, both chlorophyll a and pheophytin a biomass results

suggest that *Baetis* may be able to graze algae to lower levels than *Potamopyrgus.*

Although *Baetis* may be better able to graze periphyton to lower levels than

Potamopyrgus, *Baetis*' behavioral decisions may change the interaction in the natural

environment. That is, *Baetis* is thought to actively enter the drift when food levels reach

a certain threshold (Kohler and McPeek 1989), and rather than remaining in an area of

decreased periphyton biomass that results from the presence of *Potamopyrgus*, *Baetis*

may choose to drift and seek areas of higher food availability. By choosing to drift,

Baetis increases its probability of death by predation, decreases the relative amount of

time spent foraging, and runs the risk of drifting to an unsuitable habitat, all of which

may ultimately decrease fitness.

Objective 3: Competition experiments— In Experiment 1, *Potamopyrgus* survivorship

was greater than survivorship of *Diphetor* (t_{14}=6.51, *P* < 0.0001; Figure 6a).

Survivorship was greater for both species in the intraspecific treatment than in the

interspecific treatment (*Potamopyrgus*: $F_{1,6}$ =50.14, *P* = 0.0004; *Diphetor:* $F_{1,6}$ = 9.61, *P*

= 0.0211), indicating the interspecific competition was greater than intraspecific

competition. Additionally, mean individual growth per day (Figure 6b) did not differ

between treatments for either species (*Potamopyrgus*: $F_{1,316}$ = 0.51, *P* = 0.4757;

Diphetor: $F_{1,132} = 1.26$, $P = 0.2640$), but *Diphetor* growth was greater than that of

Potamopyrgus ($t_{199} = 5.78$, $P < 0.0001$).

In Experiment 2, the overall survivorship of *Potamopyrgus* was greater than that

of *Baetis* ($t_{37} = 8.2$, $P < 0.0001$, Figure 7). The mean survivorship for *Potamopyrgus* was

greater when maintained only with conspecifics than when combined with *Baetis* (i.e.,

B+P; Figure 7) (treatment: $F_{1,18} = 287.31$, $P < 0.0001$). Density negatively affected

survivorship only when *Potamopyrgus* was combined with *Baetis* (B+P) (density: $F_{1,18} =$

8.44, $P = 0.0095$; treatment*density: $F_{1,18} = 6.30$, P = 0.007). Similarly, the mean

survivorship of *Baetis* was greater when with conspecifics than in combined treatments

with *Potamopyrgus* (Fig 7) (treatment: $F_{1,20} = 24.01$, P < 0.0001). However, *Baetis*

survivorship did not differ between low and high densities (density: $F_{1,20} = 0.0$, P =

0.9520; treatment*density: $F_{1,20} = 0.0$, P = 0.9609).

The overall mean daily growth of *Potamopyrgus* did not differ from that of *Baetis*

($t_{1341} = 1.14$, $P = 0.2533$, Figure 7). *Potamopyrgus* growth did not differ between solitary

and mixed treatments (Figure 7, $F_{1,873} = 0.36$, $P = 0.5487$). However, increased density

negatively affected *P. antipodarum* growth (density: $F_{1,873} = 91.55$, $P < 0.0001$;

treatment*density: $F_{1,873} = 0.79$, $P = 0.376$). In contrast, *Baetis* growth did not differ

between solitary and mixed treatments nor between low and high densities (Figure 7,

treatment: $F_{1,430} = 0.15$, $P = 0.7019$; density: $F_{1,430} = 1.68$, $P = 0.1961$; treatment*density:

$F_{1,430} = 0.40$, $P = 0.5260$).

One reason we did not detect any effects of *Potamopyrgus* on the growth of

Diphetor or *Baetis* was the low survivorship of both mayflies in the experiments. Low

survivorship resulted in fewer individuals from which to estimate growth in each

replicate; i.e., a small sample size. Additionally, if we assume that only the most healthy individuals survived, these many be less affected by competition than by unhealthy individuals and result in a biased sample.

 Objective 4: Fish feeding and growth — Diet analysis of 29 *S. trutta* and 17 *C. bairdi* removed from a reach containing high snail densities ($>50,000$ m^{-2}) in 2003 yielded only 1 *Potamopyrgus antipodarum* in the stomach of a *S. trutta* (greater than 23 cm length). This *P. antipodarum* individual appeared to be a newly hatched juvenile less than 1mm in length.   Additionally, diet composition of trout and *C. bairdi* held in experimental cages seemed to change between low- and high density reaches with *Potamopyrgus*. That is, *S. trutta* tended to eat more amphipods in low-snail than in high-snail density reaches (Figure 8a). *Cottus bairdi* tended to eat a more varied diet in high-snail than in low-snail reaches, where only two taxa (Isopoda and Chironomidae) were eaten (Figure 8b).

In 2004, the diets of 34 *S. trutta* that were caught in a reach with high densities of *P. antipodarum* prior to the experiment did not contain *P. antipodarum*. However, 2 out of 15 individuals recovered from the high-snail enclosures after the experiment was terminated had 1 *P. antipodarum* each in their stomachs. Additionally, 11 out of 15 *O. mykiss* that were recovered from high-snail enclosures contained at least one *P. antipodarum* individual. The mean number of *P. antipodarum* found in *O. mykiss* was 4.8 ± 1.82 (mean $\pm$ SE).

In the 2003 fish growth experiment, *S. trutta* gained weight whereas *C. bairdi* lost weight (Figure 9; species effect $F_{1,6} = 14.16$, $P = 0.0094$). It seems probable that *C. bairdi* lost weight in this experiment due to density-dependent effects because three *C. bairdi* were held in each cage. Although growth for both species appeared higher in the low-snail reaches, there were no differences between snail reaches for either species (snail effect $F_{1,6} = 1.58$, $P = 0.2553$; species*snail interaction $F_{1,6} = 0.0$, $P = 0.9646$). High variability of trout growth in the low-density *P. antipodarum* reaches reduced our ability to detect any effect of *P. antipodarum* on *S. trutta*.

In 2004, the growth rate of both fish species did not differ between low-snail density (0.070 g d^{-1}) and high-snail density (0.069 g d^{-1}) reaches (snail effect, $F_{1,8} = 0.00$, $P = 0.95$). Additionally, the growth rate did not differ between *S. trutta* (0.061 g d^{-1}) and *O. mykiss* (0.078 g d^{-1}) (species effect, $F_{1,8} = 0.76$, $P = 0.41$; snail X species effect, $F_{1,8} = 0.00$, $P = 0.98$), even though *O. mykiss* individuals were larger than *S. trutta* at the start and the end of the experiment.

Significance of findings:

Contrary to previous research (Cada and Kerans, submitted), this study does not demonstrate a strong effect of *Potamopyrgus* on the density or biomass of baetid mayflies in the field. Factors such as high levels of patchiness (Simon and Townsend 2003) and environmental variation, in combination with the invasion process, may decrease the ability to detect the effects of species interactions at a larger spatial scale (Kerans et al. 2005). In addition, field observations did not separate different types of interactions between *Potamopyrgus* and baetid larvae, which could be a combination of both negative

and positive interactions of differing magnitudes that sum to a smaller net negative
interaction (Berlow 1999). Similarly, competitive interactions between closely related
species, such as between baetid species, may obscure the responses of baetids to *P.
antipodarum*. Furthermore, periphyton is not the only resource for which *Potamopyrgus*
may compete with baetid mayflies. Space is likely to be an important factor because high
densities of *Potamopyrgus* will limit habitat availability (Zaranko et al. 1997, Kerans et
al. in 2005).

In contrast to the field observations, the competition experiments demonstrated a
negative effect of *Potamopyrgus* on baetid mayfly survivorship. Decreased survivorship
may affect population dynamics of baetid species and may ultimately have negative
implications for the persistence of some mayfly populations in the presence of
Potamopyrgus. However, these experimental results do not agree with field observations,
which indicated no effect of *Potamopyrgus* on baetids. Experimental results do not
always agree with observational studies because factors operating at a large spatial scale
may overwhelm the importance of small-scale factors (Peckarsky et al. 1997, Thrush et
al. 1997). Additionally, extrapolation of results from an experiment to the population or
community level may also be affected by species interactions (Billick and Case 1994)
that are not included within the experiment.

Competition experiments also demonstrated a negative effect of baetid mayflies
on *Potamopyrgus* survivorship, which may adversely affect the degree of success of
Potamopyrgus populations. That is, *Potamopyrgus* densities in Darlinton Spring Creek
may be limited, at least in part, by competition with baetids. This relationship is known

as the "biotic resistance hypothesis" and has been proposed as one way to understand why invasion success varies (Baltz 1993).

Experiments and observations in this report also showed that *Potamopyrgus* can depress periphyton food resources, but whether to a level that limits other species will depend upon biological attributes and competitive abilities of each species.

Because this study does not demonstrate an effect of *Potamopyrgus* on baetid mayflies in the field, but does indicate that *Potamopyrgus* can negatively affect baetid survivorship, it forces the question—"under what circumstances might *Potamopyrgus* affect baetids, as well as other macroinvertebrates?" One working hypothesis is that *Potamopyrgus* does not negatively affect baetids until densities reach a certain level— perhaps >50,000 or >100,000 m^{-2}. An additional hypothesis may be that the effect of *Potamopyrgus* on baetids may change over time, having a greater effect during times of lower productivity (winter) or during different developmental ages of baetid larvae. For *Potamopyrgus*, as well as other invasive species, this question is important to ask and answer so that accurate predictions about the consequences of the invasive species can be made. Furthermore, we caution against interpreting the results of this study to mean that *Potamopyrgus* will not have an effect in other invaded locations.

Finally, this study does not demonstrate a strong effect of *Potamopyrgus* on the growth of either *S. trutta, O. mykiss,* or *C. bairdi*, but it does suggest that insectivorous fishes may adjust their diet according to changes in macroinvertebrate abundances caused by *Potamopyrgus*. Furthermore, *O. mykiss* frequently fed on *P. antipodarum.* However, the amount of sustenance that *P. antipodarum* contributes to the growth of *O. mykiss* individuals is still unknown. At least 50% of *P. antipodarum* were recovered from

intestines rather than the stomachs and were relatively undigested (C. Cada, personal

observation). This suggests that *O. mykiss* gut-retention time was not sufficient to digest

P. antipodarum and that they gained little energy or nutrition from *P. antipodarum*.

Publications/Citations:
The research offered in this report has been presented publicly at two conferences and at

an informal gathering between biology/ecology departments at Montana State University

and University of Montana. With the exception of the 2004 fish experiment, these data

were published in the Master's thesis of Chelsea A. Cada in 2004.

Cada, C. A. and B. L. Kerans. Submitted. Community response to *Potamopyrgus antipodarum* invasion. Biological Invasions.

Cada, C. A. and B. L. Kerans. In preparation. Competitive interactions between *Potamopyrgus antipodarum* and baetid mayflies.

Cada, C. A., B.L. Kerans, and J. Smith. In preparation. Trophic effects of the New Zealand mud snail, *Potamopyrgus antipodarum,* on trout and a sculpin.

Cada, C. A. 2004. Interactions between the invasive New Zealand Mud Snail, *Potamopyrgus antipodarum,* baetid mayflies, and fish predators. Master's thesis, Department of Ecology, Montana State University, Bozeman.

Cada, C. A. and B. L. Kerans. 2004. Competitive interactions between the invasive gastropod *Potamopyrgus antipodarum* and baetid mayflies. Annual Meeting of the North American Benthological Society. Vancouver, B.C.

Cada, C., J. Smith, and B. L. Kerans. 2003. "What about the fish?" 3rd Annual *Potamopyrgus antipodarum* Conference. Montana State University—Bozeman.

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Table 1. Experimental design of field competition Experiment 2 indicating the species and density combinations for each treatment, the number of individuals stocked per chamber, and the number of replication for each treatment. B=*Baetis tricaudatis*. P=*Potamopyrgus antipodarum*.

Species	Density	# Individuals	n
Baetis	low	120B	6
Potamopyrgus	low	120P	5
Baetis + Potamopyrgus	low	60B + 60P	6
Baetis	high	240B	6
Potamopyrgus	high	240P	5
Baetis + Potamopyrgus	high	120B + 120P	6
Control	na	0	5

Table 2. Results of repeated measures 2-way MANOVA for *P. antipodarum* (a) and
Baetidae mayflies (pooled by family) (b) where density and biomass were
repeatedly measured over time. Note that "+" indicates that instead of λ, the value
reported is the F-statistic from the between-subjects' effect repeated measures
analysis

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a. *Potamopyrgus antipodarum*

Source of variation	df	Wilk's lambda	*P*
Density			
Time	13, 16	0.106	**<0.0001**
Snail	1, 28	1926.7[+]	**<0.0001**
Time*Snail	13, 16	0.141	**0.0001**
Time*Reach(Snail)	26, 32	0.208	0.1511
Biomass			
Time	13,16	0.203	**0.0019**
Snail	1, 28	3346.6[+]	**<0.0001**
Time*Snail	13,16	0.198	**0.0016**
Time*Reach(Snail)	26, 32	0.091	**0.0027**

b. Baetidae

Source of variation	df	Wilk's lambda	*P*
Density			
Time	13, 16	0.0354	**<0.0001**
Snail	1, 28	0.24[+]	0.6248
Time*Snail	13, 16	0.542	0.4624
Time*Reach(Snail)	26, 32	0.0621	**0.0003**
Biomass			
Time	13, 16	0.0357	**<0.0001**
Snail	1, 28	0.18[+]	0.675
Time*Snail	13, 16	0.55	0.488
Time*Reach(Snail)	26, 32	0.0524	**<0.0001**

Table 3. Results of repeated measures 2-way MANOVA for *Baetis tricaudatis, Diphetor hageni* and *Acerpenna pygmaea,* where density and biomass were repeatedly measured over time. Note that "[+]" indicates that instead of λ, the value reported is the F-statistic from the between-subjects' effect repeated measures analysis.

Density				Biomass			
Source of variation	df	Wilk's lambda	*P*	Source of variation	df	Wilk's lambda	P
Baetis							
Time	13, 16	0.059	**<0.0001**	Time	13,16	0.044	**< 0.0001**
Snail	1, 28	0.1+	0.7545	Snail	1, 28	0.09+	0.763
Time*Snail	13, 16	0.485	0.3023	Time*Snail	13,16	0.444	0.2043
Time*Reach (Snail)	26, 32	0.065	**0.0004**	Time*Reach (Snail)	26, 32	0.057	0.0002
Diphetor							
Time	13, 16	0.066	**<0.0001**	Time	13, 16	0.054	**< 0.0001**
Snail	1, 28	0.51+	0.4790	Snail	1, 28	0.66 +	0.4218
Time*Snail	13, 16	0.409	0.1368	Time*Snail	13, 16	0.408	0.1358
Time*Reach (Snail)	26, 32	0.137	**0.0239**	Time*Reach (Snail)	26, 32	0.129	**0.0181**
Acerpenna							
Time	13, 16	0.055	**<0.0001**	Time	13, 16	0.059	**< 0.0001**
Snail	1, 28	1.72+	0.1998	Snail	1, 28	1.74 +	0.1979
Time*Snail	13, 16	0.453	0.2239	Time*Snail	13, 16	0.482	0.2932
Time*Reach (Snail)	26, 32	0.059	**0.0002**	Time*Reach (Snail)	26, 32	0.06	**0.0002**

Table 4. Results of repeated measures 2-way MANOVA for chlorophyll *a* and
pheophytin *a* biomass where periphyton biomass was repeatedly measured over
time. Table 4. Note that "[+]" indicates that instead of λ, the value reported is the F-
statistic from the between-subjects' effect repeated measures analysis.

Source of variation	df	Wilk's lambda	P
		Chlorophyll *a*	
Time	13, 11	0.1049	**0.0012**
Snail	1, 23	3.9600 [+]	0.0587
Time*snail	13, 11	0.2671	0.0850
Time*reach(snail)	26, 22	0.1164	0.1230
		Pheophytin *a*	
Time	13, 11	0.0491	**< 0.0001**
Snail	1, 23	1.0600 [+]	0.3136
Time*snail	13, 11	0.2740	0.0939
Time*reach(snail)	26, 22	0.0541	**0.0085**

Figure 1. - Temporal trends in the densities and biomasses (mean ± 1 SE) of *Potamopyrgus antipodarum* and Baetidae mayflies in high-snail (filled circles) and low-snail reaches (open circles). For each snail type and each time period, 16 cobble samples were taken for a total of n = 384 invertebrate samples.
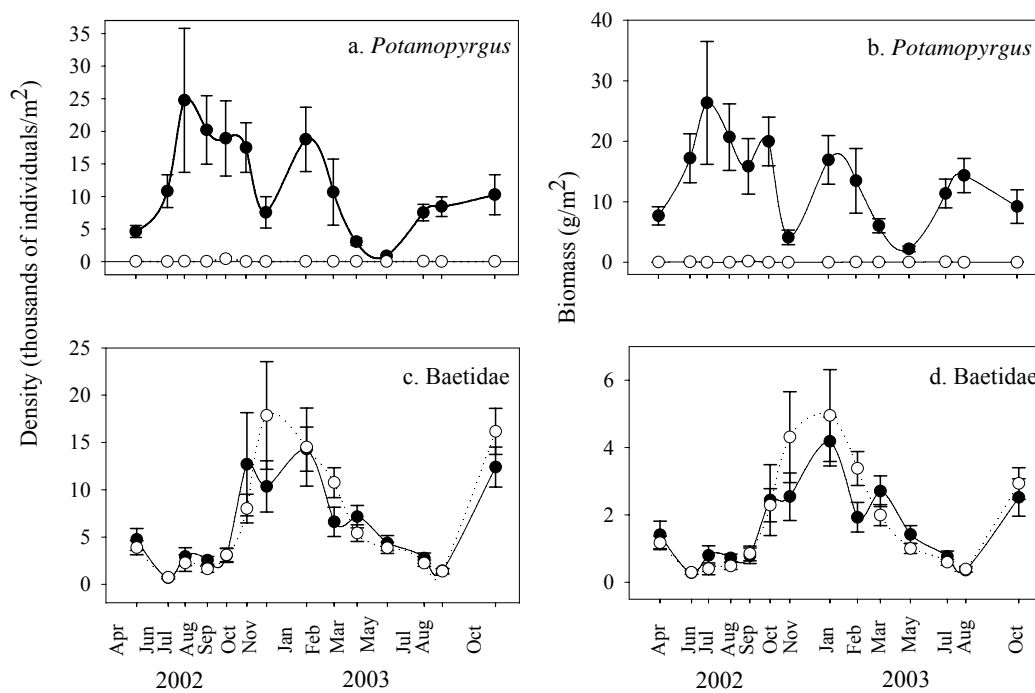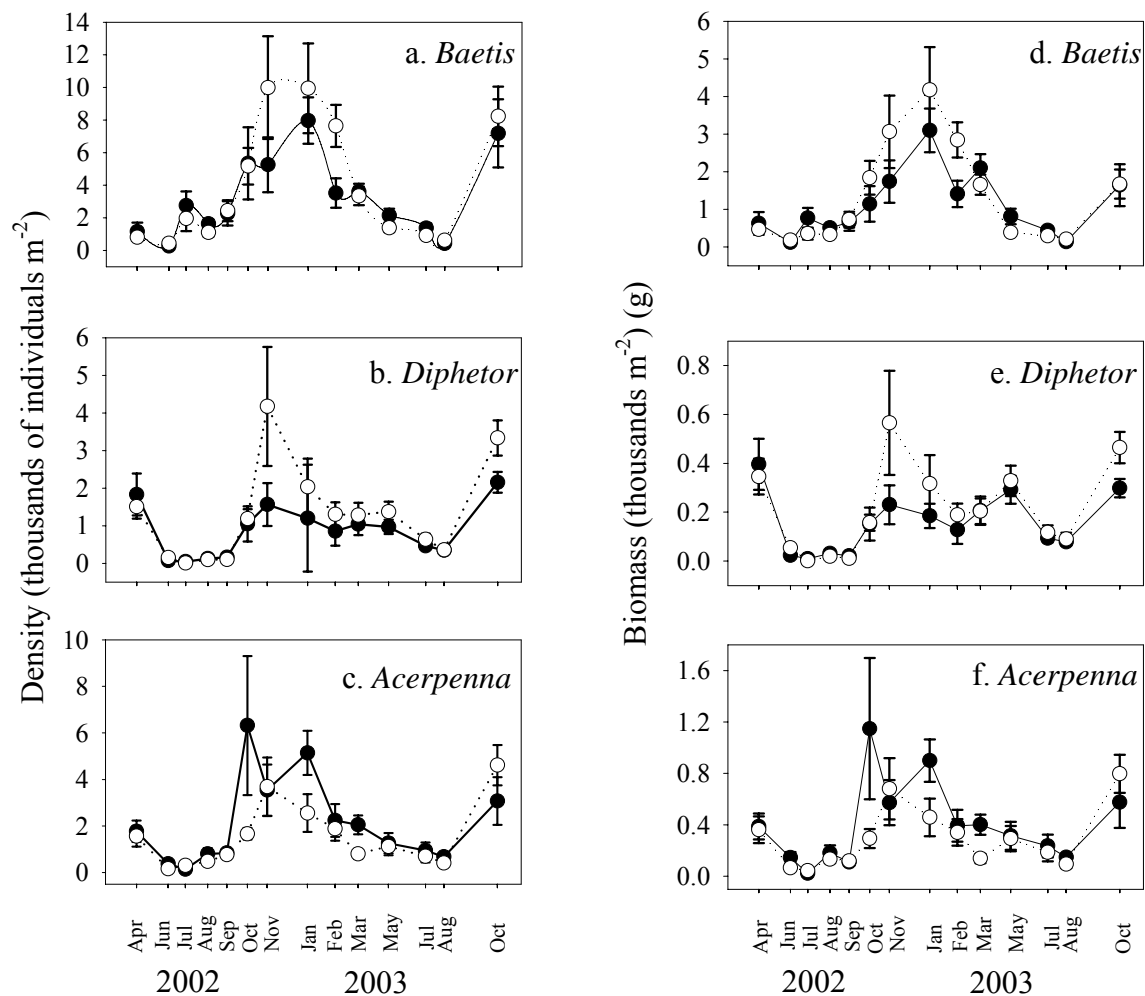
Figure 2 - Temporal trends in the densities (mean ± 1 SE) of *Baetis tricaudatis*, *Diphetor hageni*, and *Acerpenna pygmaeus* in high-snail (filled circles) and low-snail reaches (open circles).   For each snail type and each time period, 16 cobble samples were taken for a total of n = 384 invertebrate samples.

Figure 3 - Chlorophyll *a* biomass (mean ± 1 SE) (a) and pheophytin *a* biomass (b) compared between high-snail and low-snail reaches over time from the field surveys. The filled symbols represent high-snail reaches and open symbols represent low-snail reaches.
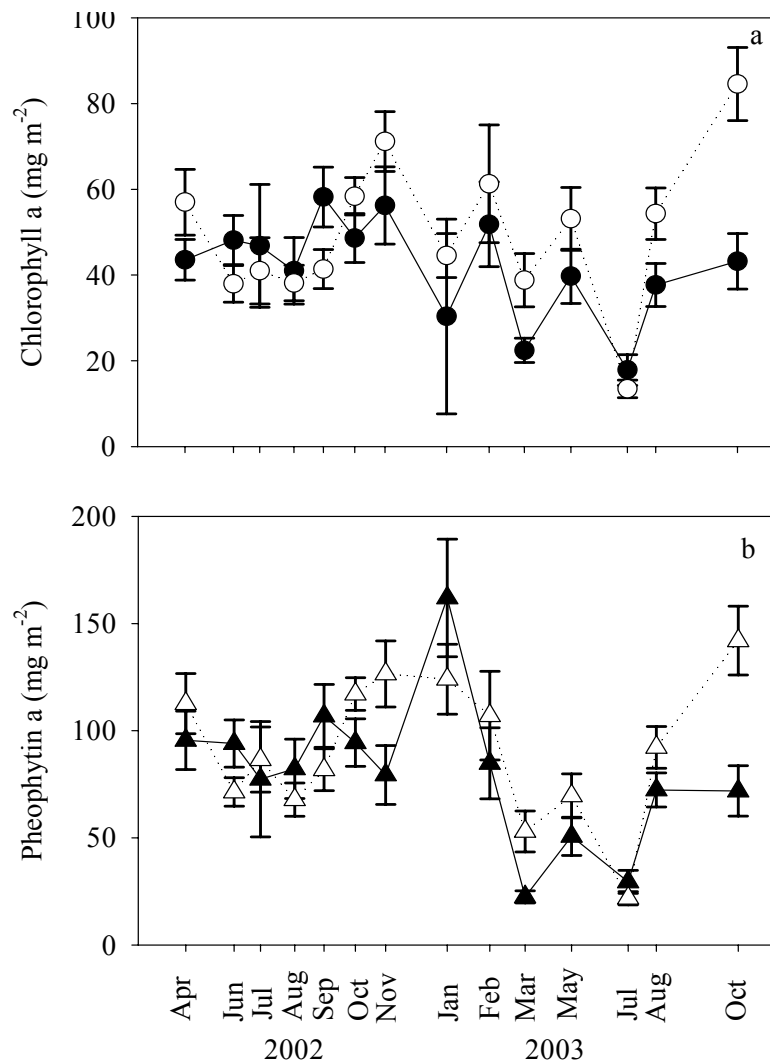
Figure 4 - Chlorophyll *a* and pheophytin *a* biomass (mean ± 1 SE) from competition Experiment 1. Treatments included biomass from the stream channel at the start of the experiment (Initial), a control with no invertebrates added (Control), *Diphetor* only (D), *Potamopyrgus* only (P), or both species (D+P). Horizontal lines indicate those treatment means that are statistically similar to each other from Tukey's HSD multiple comparisons ($p < 0.05$).
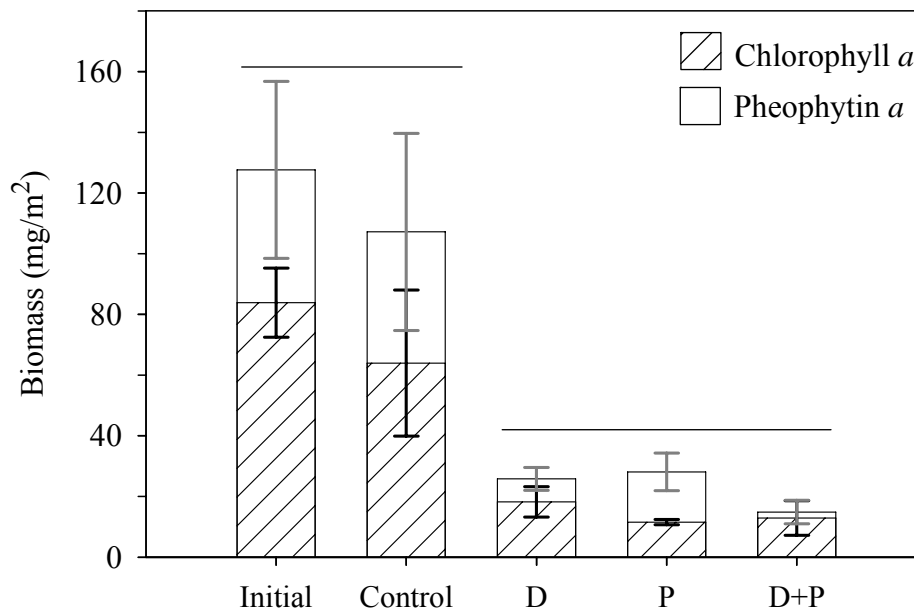
Figure 5 - Chlorophyll *a* (shaded) and pheophytin *a* (open) biomasses (mean ± 1 SE) from competition Experiment 2. Treatments included biomass from the stream channel at the start of the experiment (Initial), a control with no invertebrates added (Control), *Baetis* only at both densities (B), *Potamopyrgus* only at both densities (P), or both species at both densities (B+P).
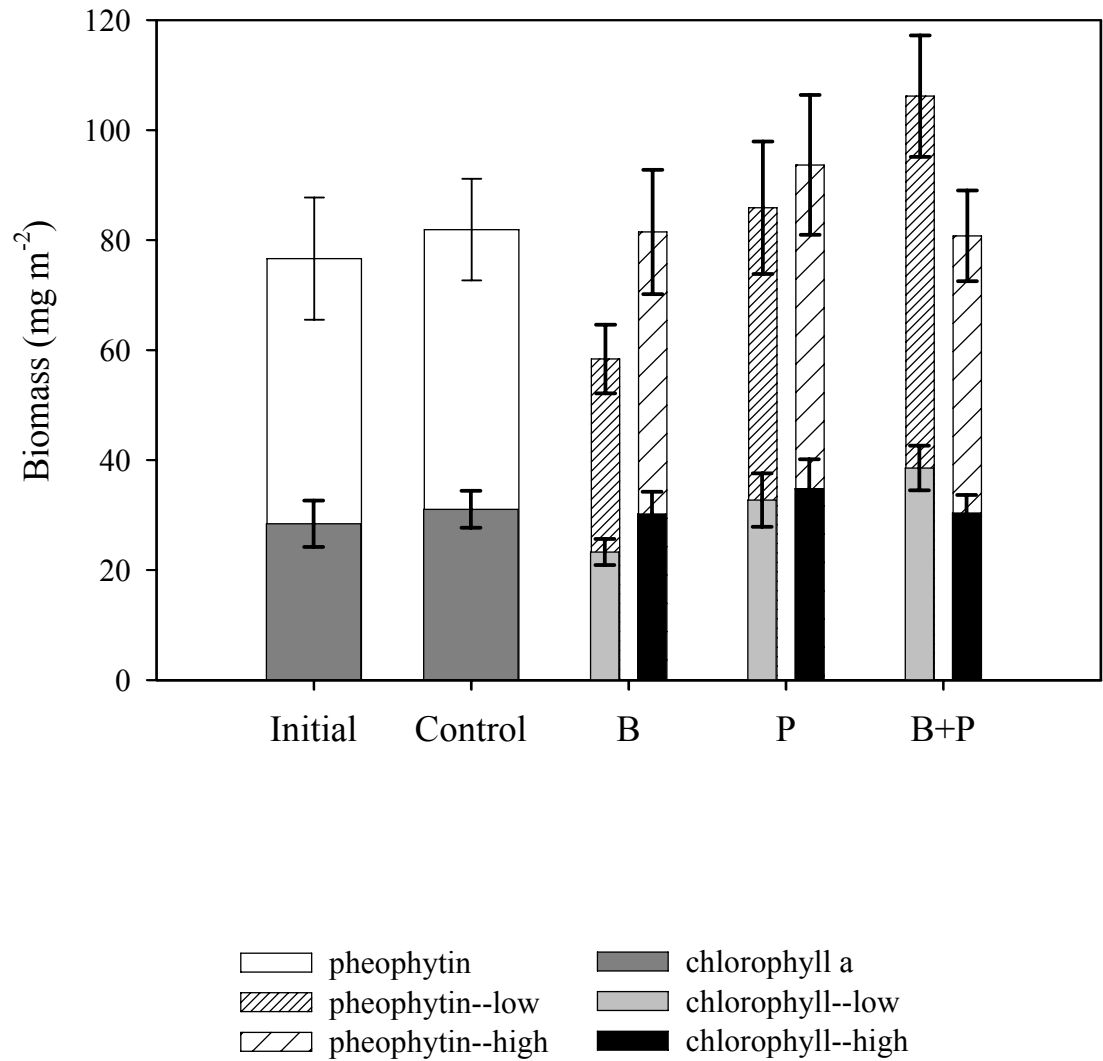
Figure 7 - Survivorship (a & b) or growth (c & d) (mean ± 1 SE) for *Potamopyrgus* and *Baetis* from competition Experiment 2. Filled circles represent *Baetis* whereas open circles represent *Potamopyrgus*. Treatments included *Baetis* only at low and high densities and *Potamopyrgus* only at low and high densities ("solitary"), or both species at low and high densities (B+P). Different upper-case letters above data points indicate differences among means using Tukey's HSD multiple comparisons ($p < 0.05$).
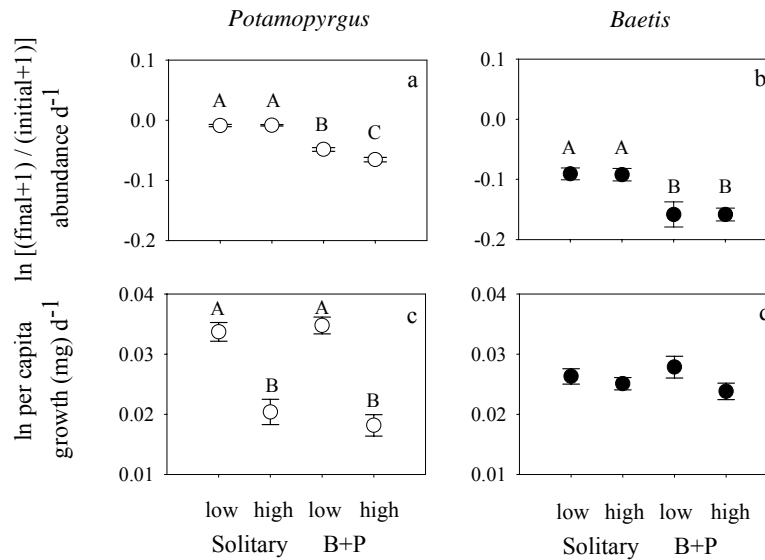
Figure 8 - The relative abundance of macroinvertebrates in stomach samples from the end of the enclosure experiment for *Salmo trutta* in high- (a) and low-snail (b) reaches and for *Cottus bairdi* in high- (c) and low-snail (d) reaches.

Salmo trutta

a) high-snail

b) low-snail

- Baetidae
- Chironomidae
- Trichoptera
- Amphipoda
- Other Ephemeroptera
- Other Diptera

Cottus bairdi

c) high snail

d) low snail

- Baetidae
- Chironomidae
- Tricorythidae
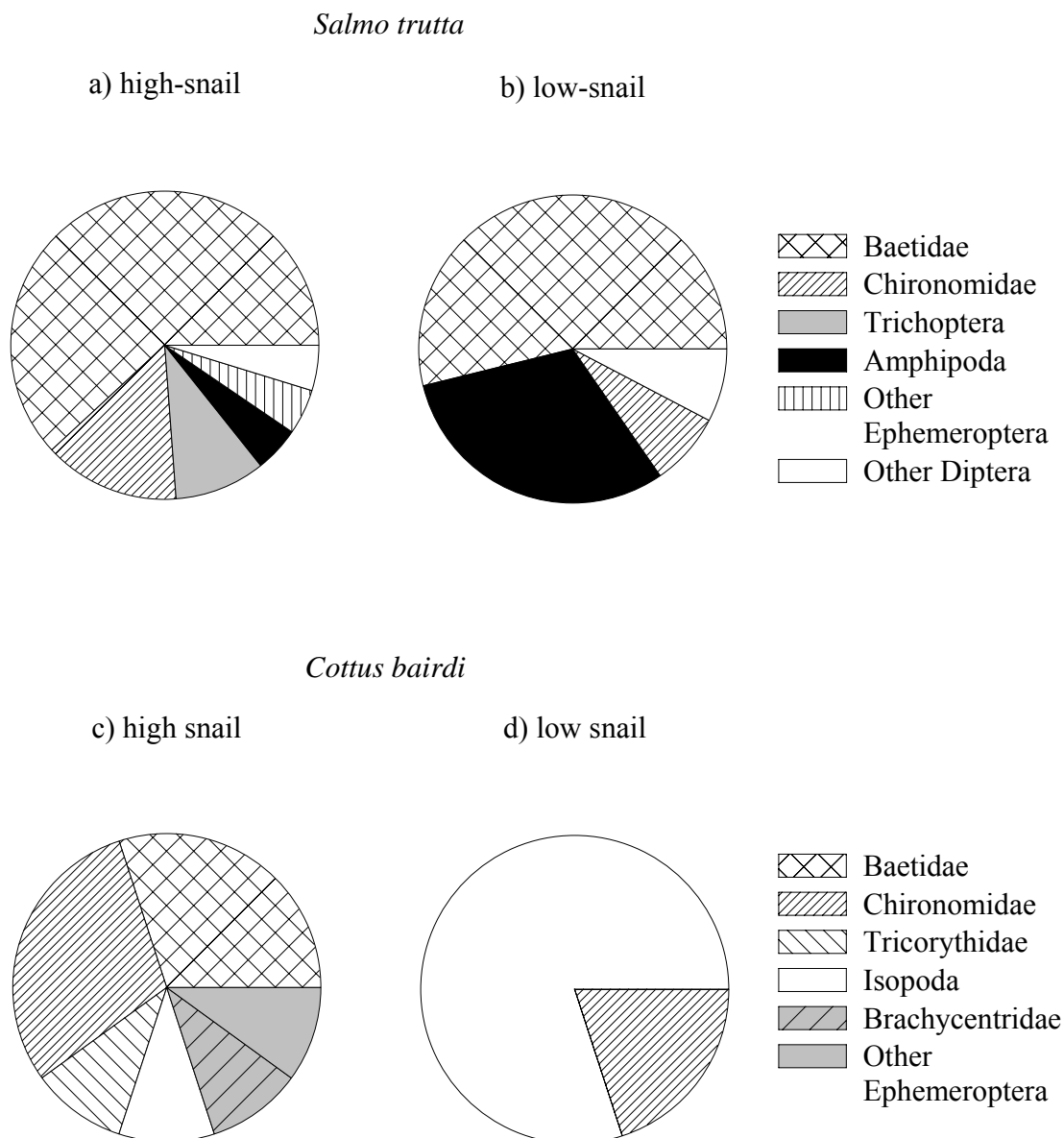- Isopoda
- Brachycentridae
- Other Ephemeroptera

Figure 9 - Comparison of fish growth in high-snail and low-snail density reaches from the enclosure experiment for *Salmo trutta* (filled circles) and *Cottus bairdi* (open circles). The dotted line represents no growth; above it is weight gain and below it is weight loss.